Adaptation to exploit nitrate in surface soils predisposes yellow-cedar to climate-induced decline while enhancing the survival of western redcedar: A new hypothesis

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ABSTRACT

Yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) and western redcedar (*Thuja plicata* Donn), two valuable tree species of Pacific Northwest forests, are competitive in low productivity forests on wet, nearly saturated soils with low nitrogen (N) availability and turnover. We propose a mechanism where cedar trees survive in marginal conditions through exploiting a coupled Ca–NO_3^- nutrient cycle where trees assimilate N as nitrate (NO_3^-), but must accumulate a counter-ion to NO_3^- such as calcium (Ca^{+2}) to control their internal cell pH and provide electrochemical balance. The availability of NO_3^- in cedar forests is favored by increased microbial activity and shifts in microbial community composition that is conducive to N mineralization and nitrification at higher pH. Cedars influence the soils under their canopy by enriching the forest floor with calcium compounds leading to increases in pH. Cedars are also prone to precocious dehardening in the spring when N is released from freeze–thaw events in the soils and conditions appear to favor nitrifying microbial communities. Cedars must concentrate fine-root biomass near the soil surface to access Ca and NO_3^-, but this beneficial physiological adaptation also creates a vulnerability to periodic root freezing injury that is leading to the decline and mortality of at least one of them—yellow-cedar.

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1. Introduction

Yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) and western redcedar (*Thuja plicata* Donn) are two important tree species that grow in the temperate rainforest ecosystems of coastal Alaska and British Columbia. Cedars are important both culturally and economically as they provide valuable wood products for Native American communities and the forest industry. The cedars are also potentially long-lived and able to withstand a diverse array of natural pathogens (Hennon et al., 2008). Yellow-cedar and redcedar often occur in mixed conifer forests and can persist and nearly dominate some forests over long periods of time (see reviews by Minore, 1983; Hennon and Harris, 1997). Both cedars reach their largest size as individual trees on well-drained soils, but appear to have a more common growth strategy of slow, prolonged survival on the fringes of bogs and other poorly drained soils where nutrient supplies are low (Krajina, 1969; Neiland, 1971; Lennon et al., 2002). Nitrogen (N) is particularly limiting to growth under these conditions and organic N is sequestered in a slowly available form in thick, undecomposed forest floors. The success of cedars on wet sites indicates that cedars have adapted to survive under conditions of low N turnover, but there is no clear explanation in the literature of the mechanisms that cedars use to successfully compete on marginal sites with unfavorable N cycling.

The extensive tree death to yellow-cedar, known as "yellow-cedar decline" occurs on >200,000 ha in southeast Alaska and has shifted the composition in these mixed conifer forests in the northern part of its range (Wittwer, 2004; Fig. 1). Initially, the decline was believed to be caused by some type of biological agent in wet soils (Hennon et al., 1990). However, there is now evidence that supports the hypothesis that the wet soils are only one of several predisposing factors related to the decline (D'Amore and Hennon, 2006). Our working hypothesis suggests that a small change in climate has led to freezing of shallow fine-roots of yellow-cedar and the development of a widespread forest decline (Hennon et al., 2008). The tendency of yellow-cedar toward

Fig. 1. Yellow-cedar decline at Slocum Arm in southeast Alaska. The dead foliage of the yellow-cedar trees creates red colors in the middle of the photo (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article).
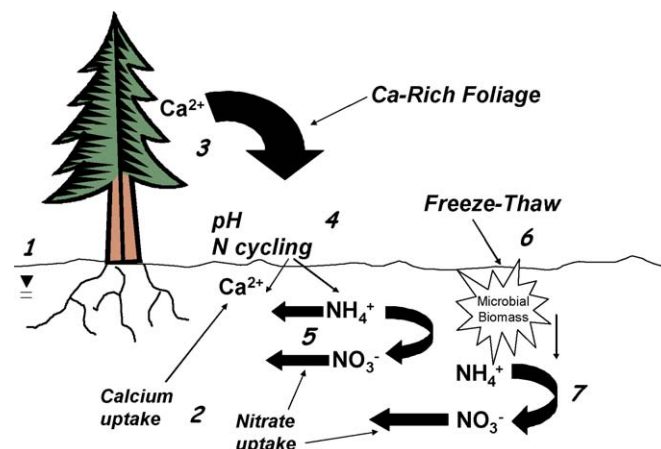

Fig. 2. Model for the hypothesis of cedar calcium (Ca) and nitrogen (N) cycling in forests of the Pacific Northwest. (1) Cedars grow in wet-soils with low N; (2) cedars assimilate NO_3^- as a nitrogen source, but must also assimilate Ca as a counter ion to balance cellular pH and osmotic pressure; (3) Ca-enriched foliage falls to the forest floor during senescence and the decomposition consumes H+; (4) increased pH enhances N turnover including nitrification in the forest floor; (5) mineralization and nitrification provide a low, but persistent supply of N to the plant along with Ca available near the soil surface; (6) spring freeze–thaw leads to the release of microbial biomass N that is nitrified; and (7) early spring dehardening and fine-root activity of cedars coincides with the N released by freeze–thaw events.

precocious dehardening in late winter and early spring (Schaberg et al., 2005, 2008) in its open-canopy habitat coincides with freeze–thaw events (Beier et al., 2008) that lead to fine-root freezing and death that have killed many of the low-elevation forests of yellow-cedar in southeast Alaska and adjacent British Columbia. While yellow-cedar has been declining in the northern part of its range over the past century as climates warm and snowcover that protect soils and roots from freezing decreases, redcedar has maintained its presence in forests. The only indication that redcedar may be subject to some type of deleterious influence of climate is the dead leaders common on large trees that have been attributed to calcium (Ca) deficiency (Walker et al., 1955). The apparent contradiction in the response of these two trees that otherwise share some similar habitat and physiological traits has led us to ask if the strategies for nutrient assimilation responsible for the survival of the cedars in marginal habitats may provide a potential clue to the vulnerability of yellow-cedar to freezing injury. The exact physical or physiological functions that are impaired or disrupted by the freezing injury are not well-understood, but the occurrence of temperatures below the cold-tolerance threshold for yellow-cedar roots (Schaberg et al., 2008) suggests that the shallow fine-roots of yellow-cedar are most vulnerable to freezing injury, which is the proximate injury leading to tree decline. The high water tables in these landscape positions presumably force fine-roots toward the soil surface where they are more vulnerable to freezing injury unless covered by snow (Hennon and Shaw, 1994; Hennon et al., 2008). However, site factors other than hydrology may also influence the growth response and activities of roots.

The goals of this paper are to provide a review on nutrient cycling of cedars and to propose a new hypothesis that explains the historic competitiveness and vulnerabilities to climate-injury of yellow-cedar and redcedar on wet sites (Fig. 2). The accumulation of calcium (Ca) and the assimilation of nitrate (NO_3^-) are two clues that may explain the rooting behavior and physiological mechanisms that lead to the competitive advantage of cedars on wet soils. We propose that the simultaneous acquisition of Ca and NO_3^- requires the maintenance of shallow roots as a competitive adaptation by cedars on marginal sites. Further, we propose that a greater predominance of superficial fine-roots of yellow-cedar relative to redcedar creates the unique susceptibility of yellow-cedar to freezing injury. The strategy and adaptive advantage of the coupled Ca–NO_3^- cycle and the implications for the cedars have not been discussed in the literature. Therefore, we reviewed available literature on mineral nutrition, nutrient contents of foliage and associated forest floors, and the general physiology of yellow-cedar and western redcedar to provide a foundation for understanding the mechanisms of nutrient cycling and use in cedar

forests to support our proposed hypothesis. We also assimilate some of our own observations with the literature review to develop, though not test, this new working hypothesis.

2. Yellow-cedar and redcedar distribution and habitat

2.1. General distribution and habitat attributes of cedars

Yellow-cedar and redcedar are abundant in the coastal temperate rainforest of the Pacific Northwest. Redcedar also has a substantial inland distribution in the Rocky Mountains in eastern British Columbia, and further south in Idaho and Montana (Minore, 1983). Yellow-cedar and redcedar populations extend north into southeast Alaska, but redcedar reaches the northern limit of its range at about 57° north latitude (USDA Forest Service, 1953). Yellow-cedar is more common at higher elevation, but also is found at low-elevation in the northern part of its range that reaches as far north as Prince William Sound (Harris, 1990; Hennon and Trummer, 2001). Yellow-cedar and redcedar expanded their presence during the cool-moist period of the latter Holocene approximately 4500 years ago (Hebda, 1983; Hebda and Mathewes, 1984). The abundance of yellow-cedar at low-elevation in the northern part of its range may be due to the existing population of trees that colonized these sites from higher elevation during the Little Ice Age (Hennon et al., 2008), a cold period that began approximately 500 years ago and persisted until the middle of the 19th Century (Heusser et al., 1985).

Biogeographic evaluations of the cedars established both as hydrophilic species that occur in wet habitats of British Columbia with >225 cm of precipitation with a great deal of the precipitation as snow to maintain soil moisture (Krajina, 1969). Yellow-cedar and redcedar grow best in areas with Ca bearing rocks (Krajina, 1969) or soils rich in Ca and magnesium (Krajina, 1969; Minore, 1983), and reach their greatest abundance and competitive status on wet, nutrient poor sites (Gregory, 1957; Krajina, 1969; Minore, 1983; Hennon et al., 1990; Hennon and Shaw, 1997), though large stature trees are also found in better-drained soils (D'Amore and Hennon, 2006). Redcedar 50 year site index in British Columbia is greatest in moist, nutrient-rich sites (Kayahara et al., 1997) and southeast Alaska where redcedar grows in moderately productive

stands with 50 year site indexes generally lower than 110 ft (Gregory, 1957). Redcedar regeneration and growth are often hindered after forest harvest in British Columbia (Weetman et al., 1989). Yellow-cedar regeneration and survival are poor in some sites (personal communication, Jim Russell, Forest Silviculturist, USDA Forest Service, Sitka, AK) and is further compromised by the widespread decline and mortality of the species in southeast Alaska (Hennon and Shaw, 1997) and British Columbia (Hennon et al., 2005). In summary, yellow-cedar and redcedar can thrive and achieve their best growth on more productive sites, yet are limited to poor sites when faced with competition from sympatric, presumably faster growing, species. The reason that cedars occupy and are competitive on marginal sites is not evident from silvicultural or mineral nutrition studies. Therefore, there must be another explanation for their competitive status on wet, nutrient-poor soils.

3. The N and Ca cycles in cedar forests

3.1. Nitrogen cycling in cedar forests

The acquisition of N in marginal sites is a key to the forest productivity and successful long-term maintenance of the cedars. The acquisition of N in saturated soils is more difficult due to (1) lower mineralization rates and (2) competition from microbial communities and bryophytes. Therefore, N availability is regulated by the ability of trees to acquire available N that is mineralized through organic matter decomposition or microbial biomass turnover. Cedar litter is N poor and N mineralization is low in redcedar forests (Prescott and Preston, 1994; Prescott et al., 2000). Redcedar forest growth is N-limited and responds well to N fertilizer treatments (Weetman et al., 1989; Bennett et al., 2003), but not liming (Prescott and McDonald, 1994). Nitrogen cycling in forests that included redcedar was lower than non-redcedar stands on Vancouver Island, BC (Prescott et al., 1993) and the authors hypothesized that the presence of redcedar was responsible for the slower decomposition of the litter in the forest floor. A subsequent study confirmed this hypothesis by demonstrating how redcedar created conditions of low N availability due to low concentrations of extractable and total N and low rates of N mineralization in the forest floor (Prescott and Preston, 1994). Generally, yellow-cedar mixes with redcedar in many stands, and although not explicitly identified, is assumed to exhibit similar nitrogen cycling dynamics.

Nitrification and the presence of NO_3^- are common in studies of redcedar nutrition and litter cycling (Turner and Franz, 1985) as NO_3^- is the preferred form of N taken up by the cedars (Krajina, 1969; Krajina et al., 1973). Nitrate production was higher in redcedar sites compared to non-redcedar sites in lab incubations of forest floors in British Columbia (Prescott et al., 2000) and in cedar forest floor samples among 16 coniferous species (Harmer and Alexander, 1986). Nitrate was assimilated in significantly higher amounts than NH_4^+ or than several organic N forms in a trial of N uptake (Bennett and Prescott, 2004). This trial demonstrated the greater uptake of inorganic forms of N compared to organic N forms, but also indicated that amino acids were an available source of N in cedar–hemlock forests. If cedars are able to exploit NO_3^- as a N source, conditions that lead to NO_3^- availability must be present in the forest floor.

3.2. Soil conditions that influence nitrogen availability: saturation, pH, and freeze–thaw

The activity of nitrifying bacteria is severely curtailed in anaerobic soils and low pH (Richards, 1987). Aerobic surface horizons coupled with increased pH provide adequate conditions for the production of NO_3^- available for uptake by cedar trees (Prescott and Vesterdal, 2005). Yellow-cedar has been found in soils with unsaturated surface acrotelm horizons (Ingram, 1983) that remain aerobic during the growing season (D'Amore and Hennon, 2006) and can promote favorable conditions for aerobic N cycling (Fellman and D'Amore, 2007). Higher pH can increase mineralization and nitrification rates, and NO_3^- may become available for assimilation by trees in acidic wetland soils (Bridgham et al., 1998; De Boer and Kowalchuk, 2001; Booth et al., 2005), which appears to be the case in redcedar forests (Turner and Franz, 1985). However, liming did not have a positive impact on N cycling (Prescott and McDonald, 1994), indicating that there may be other mechanisms that operate under natural conditions and complicate the interaction of nitrification and plant uptake of N.

Large accumulations of organic matter in cedar forests combined with the diverse and abundant microbial communities could lead to greater N release after freeze–thaw events in spring. In cold climates, freeze–thaw cycles during winter result in the release of labile organic matter in the spring derived from microbial cell lysis (Schimel and Clein, 1996). Nitrogen release after freeze–thaw is dependent on the soil organic matter quality and microbial biomass. Soils with more C, N and biomass release more N during thaw events (Schimel and Clein, 1996). The change in structure of the soil organic matter due to these physical and chemical shifts increases microbial activity (Schimel and Weintraub, 2003). Evidence from southeast Alaskan peatlands confirms that labile, protein-rich dissolved organic material is present in the spring in bogs and forested wetlands, in conditions similar to those of cedar forests (Fellman et al., 2008). Late winter and spring pulses may create a source of available NO_3^- for cedar uptake if cedar roots are active at that time.

3.3. Cedars are Ca accumulators and enrich their foliage in Ca

Numerous studies identify the distinctive trait of the Cupressaceae family, including yellow-cedar and redcedar, to accumulate Ca in their tissues (Alban, 1969; Zobel et al., 1985; Kiilsgaard et al., 1987; Kranabetter et al., 2003). High foliar Ca concentrations have been noted as the source of Ca-rich forest floors with higher pH compared to forest floors under other species (Alban, 1969; Turner and Franz, 1985). Yellow-cedar and redcedar accumulate large amounts of Ca in their tissues (Alban, 1969; Kranabetter et al., 2003) that cannot be re-translocated elsewhere in the tree because it is immobile in the phloem (Marschner, 2002). A possible pathway for enhanced Ca cycling is through interactions with bacteria and fungi. It is well established that Ca uptake and accumulation in above-ground portions of plants is driven by transpirational demand, and that root apices disproportionately allow for Ca uptake (Marschner, 2002). However, there is also some evidence that mycorrhizae may allow plants to increase Ca uptake—perhaps by the fungal associations exuding organic acids that help solubilize Ca from easily weathered substrates (Marschner, 2002; Blum et al., 2002; Yanai et al., 2005).

Foliar Ca concentrations measured at two study locations in southeast Alaska were very similar (Table 1) and consistent with previously reported foliar Ca concentrations from other studies (Fig. 3). Poison Cove (57°31′N, 135°35′W) is an intensively studied natural area of yellow-cedar decline on Chichagof Island approximately 100 km north of the northern limits of the redcedar distribution. Ward Lake (55.4°N, 131.7°W) is located within the redcedar distribution near Ketchikan, AK, and is the site of a current study of the relative cold-tolerance of roots for five conifer species including yellow-cedar and redcedar. Foliage collected from 30 mature trees (6 from each conifer species) at Ward Lake in January 2008 showed nearly identical Ca concentrations to foliage collected from 93 mature yellow-cedar and western hemlock

Table 1
Mean foliar calcium concentrations for conifer species located in southeast Alaska collected in January 2008 ($n = 24$) at Ward Lake, and two conifer species collected at Poison Cove in May 2003 ($n = 93$). Standard errors are given in parentheses. Means with different letters are significantly different within each location based on Tukey–Kramer HSD analysis at $P < 0.05$.

Species	Total foliar calcium concentration (mg/kg)	
	Ward Lake	Poison Cove
Yellow-cedar	11358.7 (810.3)[a] ($n = 5$)	11895.6 (481.6)[a] ($n = 47$)
Redcedar	7277.4 (362.0)[b] ($n = 5$)	nd
Sitka spruce	2395.1 (486.8)[c] ($n = 3$)	nd
Mountain hemlock	1982.8 (191.6)[c] ($n = 5$)	nd
Western hemlock	2449.6 (267.5)[c] ($n = 6$)	2310.6 (84.4)[b] ($n = 46$)

Methods: Nutritional analysis was assessed on the current-year foliage of hemlocks and spruce and the distal segments of primary shoots (the region assessed for physiologic comparison to current-year foliage) for cedars (Schaberg et al., 2005). Foliage was dried for two weeks at 65 °C upon return to the laboratory. Samples were ground to pass a 2 mm sieve and digested by heating with nitric acid and hydrogen peroxide using a block digester (adapted from Jones and Case, 1990), and analyzed for total foliar cations (Ca, Al, K, Mg, Mn) by inductively coupled plasma atomic emission spectroscopy (ICP-AES, PlasmaSpec 2.5, Leeman Labs, Lowell, MA). Eastern white pine needles from the National Bureau of Standards and Technology (SRM 1575), sample duplicates, and blanks were analyzed for procedural verification. Tissue standards were within 5% of certified values.
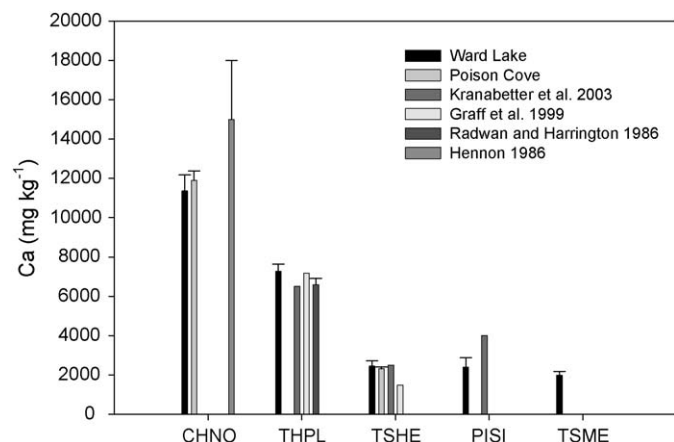*Note*: nd designates no sample taken.

Fig. 3. Foliar Ca concentrations in several conifers common to the coastal temperate rainforest. CHNO: Yellow-cedar; THPL: Redcedar; TSHE: Western hemlock; PISI: Sitka spruce; TSME: Mountain hemlock.

(*Tsuga heterophylla* (Raf.) Sarg.) trees at Poison Cove in March 2003. The distance between these two sites and the large gap between sample times highlights the consistency of foliar Ca concentrations for yellow-cedar and western hemlock. We used the same relative tissue types and analytical methods (i.e., not a source of variation) and despite potential differences due to yearly variations in transpirational demand, differences among species are remarkably consistent for the two species at the two sites we measured (Table 1). Furthermore, Ca is immobile in the phloem, so foliar concentrations are solely the result of transpirational inputs and the soil-based Ca supplies they integrate, with no redistribution of Ca from other potential plant stores. Despite consistent evidence for abundant foliar Ca, it is unclear (1) why the cedars accumulate Ca in concentrations well-above their nutritional demands (Kranabetter et al., 2003) and (2) how this accumulation may be of some adaptive benefit to cedars.

3.4. Cellular mechanisms of NO_3^- assimilation

Assimilation of NO_3^- is energetically unfavorable compared to ammonium (NH_4^+) within plants and requires the associated uptake of cations as a means to balance electrochemical potentials
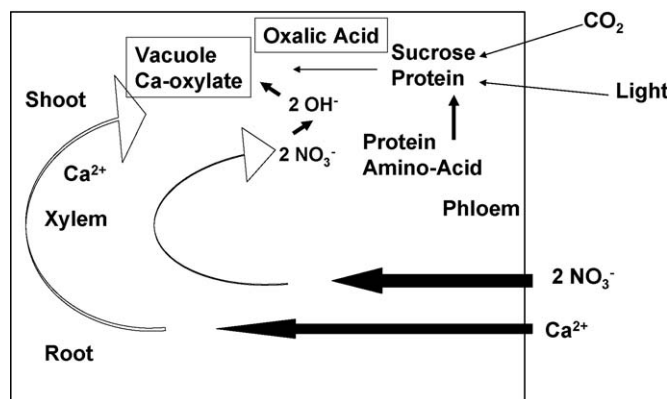

Fig. 4. The assimilation of nitrate (NO_3^-) in plants must be accompanied with uptake of a counter ion to balance internal pH and osmolarity in the plant cells. Calcium (Ca) must be transported away from the cytoplasm along with any organic acid by-products in order to avoid toxicity in the cell. Ca-oxylate is a common precipitate in cell walls (Adapted from Raven and Smith, 1976).

in plant tissues (Raven and Smith, 1976). Under these conditions there must be some compensating advantage to account for preferential uptake of NO_3^- by cedars. Cations tend to accumulate in tissues of plants that use NO_3^- (e.g., cedars) as an N source as opposed to NH_4^+ (e.g., many other conifers) (Van den Driessche, 1971; Min et al., 1998). The large uptake of N relative to other nutrients requires a plant to maintain an internal cell charge balance through cellular pH and electrochemical regulation (Fig. 4; Raven and Smith, 1976). The accumulation of NO_3^- requires a great deal of energy to reduce the NO_3^- inside the plant, nearly as much energy as N-fixation (Gutschick, 1981). An important by-product of NO_3^- assimilation is oxalic acid, which is a potentially toxic compound that must be neutralized by Ca to form Ca oxalate. Physiologists have portrayed this phenomenon as a dual detoxification process: Ca neutralizing damage by oxalic acid, and oxalic acid removing labile Ca that could bind to inorganic phosphate and disrupt ATP relations (Bush, 1995; Knight, 2000; Marschner, 2002). The mechanism of Ca and oxalate transport and precipitation outside the cytoplasm resolves both chemical threats. In redcedar, Ca is also thought to be neutralized by precipitation of $CaCO_3$ due to the low concentration of oxalic acid in this species (Graff et al., 1999).

3.5. Calcium enhances N cycling through changes in forest floor chemistry

The fall senescence of cedar foliage enriches the forest floor with Ca. This is also the case of dying yellow-cedars that drop their entire compliment of foliage to the forest floor (D'Amore and Hennon, 2006). The accumulated Ca in cedar tissue becomes a source of acid neutralizing capacity by replacing H^+ ions on soil exchange sites with Ca when shed organs decompose. This process raises the pH of the forest floor (Alban, 1969; Turner and Franz, 1985; Prescott and Preston, 1994; Prescott et al., 2000). The increase in pH would directly benefit nitrifying organisms, but appears to also promote NH_4^+ oxidizing bacteria (Turner and Franz, 1985). There is evidence that the Ca-enriched litter changes the soil organic matter chemistry in the forest floor below cedars (Klinka and Lowe, 1975). The forest floor chemistry in a cedar forest in British Columbia exhibited higher protein content in organic matter compared to western hemlock and Douglas-fir forests (Klinka and Lowe, 1975). The presence of proteins may be an indicator of microbial turnover or mineralized soil organic matter. This is similar to the 'protein peak' identified in spectrofluorometric analysis of dissolved organic matter from wet soils of

northern southeast Alaska which was attributed to higher microbial biomass in spring (Fellman et al., 2008). The altered soil organic matter structure influences the microbial community (Turner and Franz, 1985; Grayston and Prescott, 2005) and provides a feedback loop for NO_3^- availability to cedars through increased N mineralization and nitrification.

The change in the chemistry of organic matter may be fairly localized and potentially seasonal given conditions in wet-forested cedar communities. The cedar foliage on the forest floor may lead to higher biological activity and decomposition rates relative to sites without cedar. However, Prescott and Preston (1994) found that redcedar litter decomposed at the same rate as western hemlock and Douglas-fir during the first 50 weeks of incubation, but then decomposed significantly faster for the duration of the experiment. The slow initial decomposition rate of redcedar was confirmed in a subsequent replicated study, but the rate of decomposition was not correlated with N mineralization (Prescott et al., 2000). The chemistry of soil organic material and decomposition rate appear to be inconsistent with the overall N cycle dynamics in cedar forests. However, there is evidence of an interaction between Ca and NO_3^- in soil nutrient cycles (Homann et al., 1994) and that these cycles can manifest themselves as distinct signatures in stream chemistry from watersheds (Christopher et al., 2005; Perakis et al., 2006).

4. Competitive status of cedars in wet soils is influenced by nutrient cycling dynamics

4.1. Nutrient cycling and the advantage of shallow roots in cedar communities

In a review of the influence of tree species on forest floors, Prescott and Vesterdal (2005) concluded that cedar forest floors were higher in pH and Ca, promoted high bacterial biomass, and contained high proportions of NO_3^- in spite of low N concentrations and low net N mineralization relative to comparable non-cedar forest floors. Prescott and Vesterdal (2005) also concluded that NH_4^+ and NO_3^- were more closely related to pH, Ca concentrations and soil biological communities than the N concentration in the litter and forest floor. These findings are consistent with assertions that the cedars are both responding to the coupled Ca–NO_3^- cycle, as well as providing an essential feedback to facilitate the continuation of the cycle.

Shallow organic soils may provide the most beneficial rooting zone for cedars due to the availability of NO_3^- and the presence of a counter ion (Ca) to balance the charge uptake. If cedars use NO_3^- as a N source, then assimilation of NO_3^- must be done either continuously over the entire growing season, or sporadically during specific growth periods. The positive feedback from cedar foliage promotes a slow-release fertilizer effect in the low-nutrient environments. N mineralization and nitrification are enhanced by the increased pH caused by Ca deposited on the soil surface by cedar foliage. In addition, a pulse-dose of N may come through large quantities of available N that are nitrified in early spring through the freeze–thaw process. In this case, shallow roots and early growth would provide competitive advantages for the cedars.

There is very little information on the rooting habit of yellow-cedar, but it may be similar to redcedar. The higher accumulation of Ca in the foliage of yellow-cedar relative to redcedar and other co-occurring species (Hennon, 1986; Fig. 3) suggests that yellow-cedar may preferentially access Ca-rich surface soils with its fine-root biomass. The potential habit of producing shallow fine-roots by yellow-cedar was previously described in our conceptual model (Hennon et al., 2008) as a response to wet, anaerobic conditions in these declining forests. Yellow-cedar (Hawkins et al., 1994; Schaberg et al., 2005, 2008), and redcedar (Grossnickle and

Russell, 2006) break cold-hardiness early in the spring. For at least yellow-cedar, this trait may represent an adaptation to high-elevations where snow consistently protects roots during the winter but trees may benefit from rapid growth and physiological activity immediately after spring snowmelt. In order to grow quickly, this adaptation also gives yellow-cedar a competitive advantage in wet locations prone to an early spring flush of N in the form of NO_3^-.

4.2. The enigma of redcedar and freezing injury

The distribution of yellow-cedar decline is well-documented through southeast Alaska (Wittwer, 2004) and British Columbia (Hennon et al., 2005). Though redcedar often grows mixed with yellow-cedar, it does not show the same widespread tree mortality problem. Redcedar has a similar pattern of early dehardening and its habit of shallow rooting (Silim and Lavender, 1994) appears consistent with our nutrient cycling hypothesis. So, why is redcedar not dying from the same factors that kill yellow-cedar? There is some evidence that redcedar is not uniformly shallow rooted (Bennett et al., 2002). Fine-root biomass of redcedar was located in both surface organic and deeper mineral horizons compared to western hemlock and salal (Gaultheria shallon Pursh) in mixed stands (Bennett et al., 2002) and peaked in the upper most mineral soil in pure cedar stands (Wang et al., 2002). Redcedar foliar Ca concentrations are less than those for co-existing yellow-cedar (Fig. 3), which may be an indicator that redcedar is not exploiting surface soil horizons to the same degree as yellow-cedar. If both cedars use the Ca–NO_3^- strategy, then the differences observed in the Ca concentration in the foliage of these species may be an indication that the rooting habitat varies in each species as well. Although shallow rooting would better support spring Ca and NO_3^- uptake, superficial rooting would also increase the vulnerability of roots to freezing injury when soils are not protected by snowpack.

This tradeoff may account for the increased susceptibility of yellow-cedar to freezing injury compared to redcedar on wet soils. If redcedar harbors fewer fine-roots in upper soil horizons and more roots in deeper mineral soil strata where Ca is less abundant, then redcedar may be somewhat less vulnerable to root injury associated with superficial freeze-thaw events. A lesser vulnerability, however, does not mean that redcedar would be immune to root freezing injury and some associated foliar dieback. It is possible that redcedar is injured, but the damage is less severe and expressed differently than seen in yellow-cedar. Indeed, dead tops, or "spike-tops" are a common feature of mature redcedars and may be an indicator of some limited root damage. The leaders of redcedar often die and are replaced later by new leaders, leading to the common forked-top or multiple-top appearance of trees. Such browning and death of leaders in redcedar seedlings is typically considered to be a symptom of Ca deficiency (Walker et al., 1955; Krajina, 1969). We speculate that the leader death in mature redcedar trees could be the result of freezing injury to fine-roots. The loss of fine-root mass would decrease the uptake of both Ca and NO_3^- according to the proposed nutrient hypothesis.

4.3. Implications for succession in declining yellow-cedar forests

The presence of shallow, fine-roots in yellow-cedar is one of the key features that cause vulnerability to freezing injury and ultimately lead to its widespread decline. Decline occurs in the same locations where yellow-cedar has previously been well-adapted and most competitive, and our recent research has outlined and tested several aspects of an hypothesis linked to freezing injury (Hennon et al., 2008). Open canopies lead to greater exposure and associated temperature changes that in turn lead to

soil freezing events and root freezing injury. Subsequent crown deterioration and eventual tree death create new open canopy conditions that facilitate temperature-induced freezing injury. Snowpack insulates soils from temperature fluctuations and hard freezes, but depths of snowpack at lower elevations in northern latitudes have declined during the 20th century (Beier et al., 2008). The proximate injury of yellow-cedar is by the death of shallow fine-roots that we propose are an adaptation to the mineral nutrition strategy developed by cedars.

Despite the widespread extent of yellow-cedar decline in southeast Alaska and British Columbia, the successional pathways in declining stands are not well-understood. We are just beginning to appreciate the influence of numerous dead cedars on remaining plant communities and watershed nutrient export. Redcedar has the potential advantage in replacing declining yellow-cedar where they grow together due to the Ca–NO_3^- feedback loop. In the southern portions of southeast Alaska, we have observed abundant vigorous-appearing redcedar growing under the large dead yellow-cedars. The mixed yellow-cedar and redcedar stands maintain forest conditions, and our observation suggests that the redcedars may replace yellow-cedars where they coexist. Yellow-cedar decline may benefit the surviving redcedar in more productive forests and encourage the development of redcedar growth due to the advantage of the Ca–NO_3^- feedback combined with crown release that accompanies mortality-induced stand thinning. This may be the reason that yellow-cedar decline was only recently recognized in British Columbia (Hennon et al., 2005) where dead yellow-cedar is obscured by healthy redcedar. The long-term health of redcedar in these declining stands should be monitored to determine if they will experience freezing problems as they grow older. In contrast, western hemlock does not respond as favorably to yellow-cedar decline, possibly because western hemlock is not able to exploit the nutrient cycling conditions favorable to cedars. Declining yellow-cedar forests in northern sites (where redcedar is absent) appear to convert to scrub forest or open bog following yellow-cedar decline. There may be some forest conversion to western and mountain hemlock, but these trees do not appear vigorous, perhaps because they are unable to tap into the NO_3^- form of N on these wet soils.

5. Climate and risks due to the mineral nutrition of cedars

5.1. Integration of the nutrient model with yellow-cedar decline scenario

Yellow-cedar is vulnerable to root freezing injury in the late winter and spring because of early dehardening and lack of protection from either snow or canopy cover (Hennon et al., 2008). Yellow-cedar roots near the surface are vulnerable to injury at fairly mild subfreezing temperatures (i.e., -5 °C; Schaberg et al., 2008). Soil freezing below the threshold for root injury to cedars is less common at 15 cm depth than 7.5 cm (Hennon, unpublished data).

Our nutrient cycling model implies that cedar roots located near the surface in wet sites are able to obtain mineralized N. These surface conditions are also more prone to the beneficial influence of foliar residues in providing a counter ion (Ca) to accommodate NO_3^- uptake. The early dehardening of yellow-cedar allows fine-roots near the soil surface to access rich soil organic matter in spring. The unique ecological niche we propose would allow cedars to enhance their growth and survival relative to other conifer competitors such as spruce and hemlock that rely on NH_4^+ uptake and sequester little Ca on wet soils. This strategy works as long as roots are protected from deleterious winter and spring temperature minima that freeze surface soils below root cold-tolerance thresholds that induce root injury. Historically,

consistent snowpacks have limited soil freezing and protected roots from extensive damage. Indeed, snowpack is linked closely to the pattern of decline on a regional scale. However, reductions in snowpack during the 20th century have influenced the growth patterns of yellow-cedar and are now believed to be a leading risk factor for decline (Beier et al., 2008). Thus, the shallow depth and precocious spring activity of roots that traditionally enhanced the competitive status of yellow-cedar on wet soils may now be a critical link to its apparent vulnerability to injury and decline.

5.2. Strategies for yellow-cedar management

Access to adequate Ca supplies may reduce the likelihood of freezing injury for yellow-cedar in a manner similar to those documented for red spruce in the Northeastern US (Schaberg et al., 2000; Hawley et al., 2006; Halman et al., 2008). However, the fine-root mass used by trees to access NO_3^- still needs to be located in the aerobic portion of the soils during the growing season that are vulnerable to greater freeze–thaw cycling when snow cover is lacking. It is unclear how much increased Ca nutrition can boost yellow-cedar cold-tolerance levels relative to the increased risks of freezing stress when snow packs are low. Deep, Ca-rich soils would alleviate the risk of near-surface freezing injury while allowing the cedars access to needed nutrients. Thus, one adaptive strategy is to favor the conservation and management of yellow-cedar on sites with better drainage. Active planting and thinning for yellow-cedar may be needed to aid yellow-cedar in its competition with other fast-growing conifers on these sites.

An adaptation strategy for yellow-cedar is to exploit suitable habitats that could serve as refugia for the maintenance of biological diversity of the species. Yellow-cedar is closely associated to Vietnamese cedar (*Xanthocyparis vietnamensis*), which was recently discovered on remote karst cliffs in northern Vietnam (Averyanov et al., 2002; Farjon et al., 2002), presumably areas of refugia for the rare tree. The Ca-rich karst landscapes in southeast Alaska may provide refugia and potential sites for viable plantations for yellow-cedar forests, as large-stature yellow-cedar and redcedar have been observed growing in these habitats.

6. Conclusions

We have addressed several of the questions posed in this review and are now beginning to understand how cedars are competitive on marginal sites. A competitive advantage for the cedars is the ability to combine the assimilation of NO_3^- as an N source with the accumulation of Ca in plant tissues. Cedars occupy a niche between open peatlands and productive forest. The Ca in foliage returned to the forest floor provides a feedback for the enhanced production of NO_3^- in low-nutrient conditions and provides a slow, but persistent N supply. A pulse of N in the spring caused by the accumulation of labile microbial material produced during freeze–thaw events is exploited through precocious dehardening by the cedars. These competitive adaptations come at the risk of freezing injury to shallow roots, which was hidden as long as snow protected fine-roots from injury. Yellow-cedar expresses this injury as mortality, while redcedar may show only limited injury. Though a complete understanding of soil nutrient cycles in these forests has not been reached, our working hypothesis provides a means for designing experiments to explain the possible successional pathways of cedars related to soil nutrient cycles. Future studies that focus on the rooting habit of yellow-cedar and redcedar along with N mineralization rates associated with microbial communities and cedar physiology will be needed to test our ideas about how the cedars are competitive on marginal sites, and evaluate associated vulnerabilities to climate change.

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